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DIRECTIONS AND TIMING OF GREAT BLUE HERON FORAGING FLIGHTS FROM A CALIFORNIA COLONY: IMPLICATIONS FOR SOCIAL FACILITATION OF FOOD FINDING

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Patterns of foraging trips of several species of colonially nesting birds have been examined recently for evidence that colonies serve as "information centres" to assist the members in finding food (Krebs 1974, Hoogland and Sherman 1976, Snapp 1976, Custer and Osborn 1978, Erwin 1978). According to this hypothesis colonial nesting is advantageous for species depending on food that is unevenly distributed and concentrated in areas of temporary abundance. Individuals who have difficulty finding food are able to follow their more successful neighbors to good feeding sites, thus reducing searching time and enhancing feeding success (Ward and Zahavi 1973).

Krebs (1974) found that Great Blue Herons (*Ardea herodias*) in a colony near Vancouver, British Columbia, tended to depart for intertidal feeding grounds in groups and birds from neighboring nests were likely to feed in the same areas on the same days. He suggested that less successful herons may have followed more successful individuals from the colony to areas of prey concentration. Although the statistical analysis of heron departures suggests that herons may follow each other on foraging trips, tracking individual birds as they leave the nest provides a more direct test of this hypothesis.

This paper presents data on timing and directions of departures taken by breeding herons as they flew to feeding grounds from nests in a central California heronry. The results are analyzed for evidence of following and for information about the degree of colony dependence on the adjacent estuary for food.

METHODS

The heronry was located in a narrow canyon at Audubon Canyon Ranch about 5.8 km north of Stinson Beach, Marin Co., California. The herons nested approximately 24–30 m from the ground in the tops of coast redwoods (*Sequoia sempervirens*) that grew in the bottom and up the north facing slope of the canyon. Bolinas Lagoon, a shallow 570-ha estuary opening onto the Pacific Ocean, lies at the mouth of the canyon to the west (Fig. 1). Behind the heronry to the east a steep ridge of mountains separates the shore from populated areas adjoining the northern stretches of San Francisco Bay.

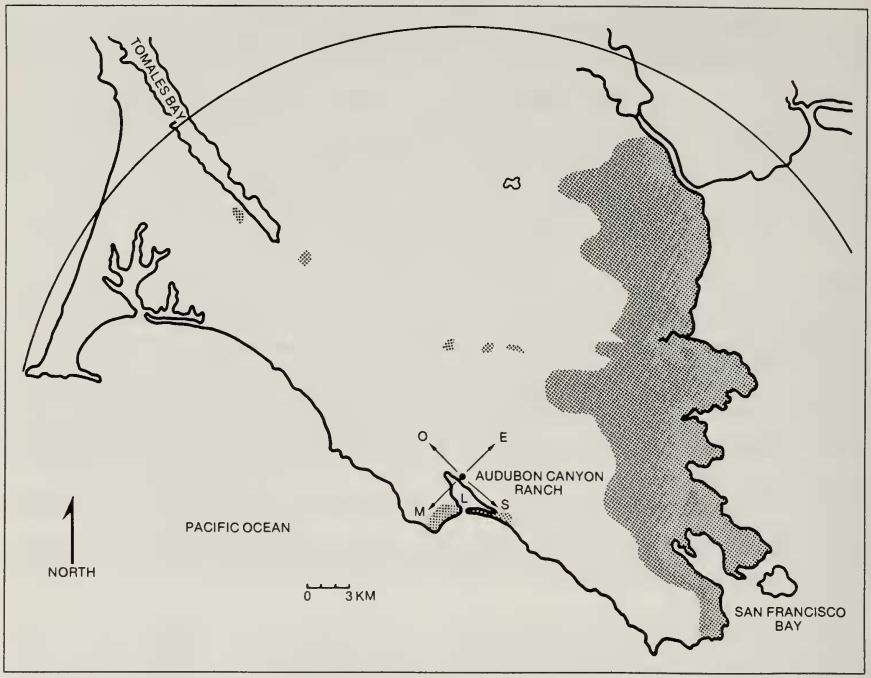

FIG. 1. Map of Marin County showing the location of the heronry at Audubon Canyon Ranch with directions taken by departing herons: L = lagoon, S = south, E = east, O = Olema Valley, M = Bolinas Mesa. Shading indicates populated areas. The arc encompasses the area within 30 km from the heronry.

The herons were observed from an overlook on the south facing slope of the canyon above the level of most nests and about 90–180 m from them. Due to the distance and/or habituation of the herons to humans at the overlook, observers caused no detectable disturbance in heron behavior.

I identified nests by plotting and numbering them on a panorama of the heronry. A team of observers tracked herons as they flew from the colony. Two persons stationed at the nest overlook recorded the time a heron flew, the nest number when possible, and in a few cases where plumage differences enabled differentiation of members of the pair, they noted which individual left. Other observers stationed on a hill overlooking the lagoon at a spot about 275 m from the nest overlook and within view of it recorded the time the heron was sighted, its direction and, for those landing in the lagoon, its destination on a map divided into quadrats of 387 m^2. Except for the first 2 sessions when it was necessary to use arm signals, the teams communicated with each other by portable CB transceivers. All observations were taken with 7× binoculars and 20× spotting scopes.

The teams tracked herons once weekly from 14 April through 2 June 1976, and from 22 March through 24 May 1977, on 16 different days. Observations from 12 May 1976, are not included in this analysis because, due to unusually hot weather, some herons on leaving the nests went directly to a drinking spot rather than hunting for prey (Pratt 1977). This behavior

TABLE 1
NUMBER OF HERON DEPARTURES IN THE OBSERVED DIRECTIONS

	1976	1977	Total	Percent
Lagoon	20	14	34	45
Olema Valley	8	7	15	20
South	8	5	13	17
Bolinas Mesa	4	4	8	10
East	2	4	6	8
Total	42	34	76	100

is considered atypical since we did not see herons going out to drink on other days. We tracked herons in the morning on 7 days between approximately 09:30 and 12:00 for a total of 11 h 30 min; afternoon observations included here were made between 13:30 and 18:00 on 8 days for a total of 14 h 55 min.

Breeding pairs numbered 40 in 1976 and 41 in 1977. Most herons were either incubating eggs or attending chicks fewer than 4 weeks old at the time of tracking.

RESULTS

Departure directions.—We tracked 76 foraging herons for the 2 years combined (Table 1). I identified the nests of 57 departing herons; 19 others left from perches in trees. I distinguished individuals from their mates by differences in crown plumage on 12 departures.

The herons flew in 5 clearly distinguishable directions (Fig. 1). The relative frequency of directions taken was essentially the same in both years (Table 1). Bolinas Lagoon was the most frequent destination (45% of departures). A flight path northwest above the Olema Valley was second in frequency (20%). All but 1 of the herons taking this route flew until out of sight. The 1 bird that was the exception to this flight pattern landed in a pasture near the north end of the lagoon. The herons that flew south (17%) followed the western edge of the coastal hills; 5 (7%) veered east before being lost to view. Those flying over Bolinas Mesa (10%) either continued northwest up the coast or landed in pastures on the mesa. Those flying east (8%) circled above the heronry many times, for up to 11 min, gaining altitude until they flew over the ridge that rises to a height of 460 m behind the heronry.

We tracked only 1 individually identified heron more than once. On 3 different days this bird flew directly to a channel bordering the road on the east side of the lagoon. This bird did not join groups of feeding herons even when they were present. Of the remaining herons that went to the lagoon, 11 landed near other herons.

Intervals between departures.—If the herons at Audubon Canyon Ranch

TABLE 2
NUMBER OF DEPARTURES AT DIFFERENT INTERVALS

Intervals (min)	No. of departures
1–4	15
5–8	13
9–12	9
13–16	8
17–20	3
21–24	5
25–28	1
29–32	1
>32	7

followed each other to feeding grounds, directions taken on successive departures would be the same and intervals between departures would be short. Since most herons either landed in the lagoon or flew out of sight within 4 min of departure, I grouped departures into 4-min intervals to analyze for evidence of following (Table 2). Only 3 of the 15 herons that left within 4 min of another went in the same direction as the preceding bird, all going to the lagoon. One landed near the leading bird and displaced it. The others landed in different areas from the preceding heron. Thus during the time of these observations breeding herons showed no tendency to follow each other on leaving the colony.

Timing of departures.—Herons that were incubating or attending small chicks usually left promptly when relieved. In 53 instances of nest relief, 40 (75%) of the relieved herons left within 5 min or less. A bout of twig presentations followed nest relief at 5 of the 13 nests where the heron lingered. Of 23 arrivals at nests with chicks old enough to be left unattended except for feeding, 7 (30%) left at once. The others remained perched on branches preening or resting often for the duration of observations.

Relation of departure directions to tide.—The data in this study do not show that the direction of departing herons differed with the tides (Table 3). About the same number of birds went to the lagoon on ebbing as on flowing tides and frequency of departures in the other directions showed no tide related trends.

DISCUSSION

The timing of departures and directions taken by the herons leaving the colony at Audubon Canyon Ranch indicated that they were behaving independently rather than following other birds. The hypothesis that follow-

TABLE 3
DIRECTIONS OF DEPARTING HERONS ACCORDING TO TIDE

	Ebbing	Flowing	Slack
Lagoon	15	17	2
Olema Valley	5	6	4
South	5	5	3
Bolinas Mesa	4	2	2
East	4	2	0
Time observed	12 h 10 min	10 h 50 min	3 h 25 min

ing is advantageous assumes that successful individuals lead others to locations of previously discovered food abundance (Ward and Zahavi 1973). This strategy would be effective where food resources are temporarily abundant but spatially confined, e.g., in ponds subject to seasonally diminishing water levels as described by Kushlan (1976). There is a difficulty, however, in applying this hypothesis to Great Blue Herons using estuarine feeding grounds where prey concentrations can change both spatially and temporally relatively quickly. During incubation and for the first 3–4 weeks of the nestling period Great Blue Heron parents usually remain at the nest until relieved by the mate (Pratt 1970). Thus, departure for the feeding grounds at this stage in the breeding cycle is determined primarily by nest relief. Nest relief usually occurs only once or twice during the daylight hours and attentive spans are long. During incubation, spans of 12 h or more are common. I have observed, after hatching, spans of 4–9 h (Pratt 1970, unpubl.) and some could be longer. Since herons at continuously attended nests remain there for several hours after arrival, prey concentrations exploited on 1 foraging trip could disperse or move before the next trip; feeding grounds accessible at low or medium tides could become inundated. Under these circumstances the quickest way to find food might be to search for and join other feeding herons. Krebs (1974) demonstrated that herons are attracted to others on the feeding grounds with the result that aggregations build up where food is plentiful through local enhancement. An alternative might be to fly directly to familiar feeding grounds known to be accessible most, if not all, of the time.

The limited data presented here suggest that the Audubon Canyon Ranch herons selected foraging spots in 2 ways. Some landed near others in the lagoon, apparently attracted by conspecifics. They were perhaps exemplifying the process of build up of feeding aggregations through local enhancement, similar to those reported by Krebs (1974). Heron feeding aggregations have also been reported by Palmer (1962), Kushlan (1976),

Willard (1977) and Bayer (1978). The direct, purposeful flight of those flying in other directions and the observation of the heron that went to the same general area in the lagoon on 3 different days suggest that other individuals went directly to favorite feeding areas. Herons have been reported to return to the same feeding sites repeatedly (Owen 1955), to feed solitarily (Bovino and Burtt 1979), and under some circumstances to defend feeding territories (Palmer 1962, Hedeen 1967, Krebs 1974, Bayer 1978).

A heron was seen catching pocket gophers (*Thomomys bottae*) on several days during the breeding season of 1978 in a field about 0.5 km from the heronry (J. Church, pers. comm.). Only 1 bird was present in the field at a time, but it was not identified and impossible to determine whether the same individual returned repeatedly.

Promptness of departure for the feeding grounds was related to the stage in the nesting cycle. Herons incubating or attending small chicks tended to leave at once, whereas herons from nests with older, unattended young were more likely to linger in the heronry. Delayed departure could be interpreted as indicating that lingering herons were waiting to follow more successful birds to feeding grounds as speculated by Krebs (1974:110). On the other hand it might indicate low motivation to search for food. Birds from continuously attended nests were limited in available foraging time and would likely be under pressure to leave for feeding grounds immediately on relief. Herons from nests with unattended young had more time for hunting and after a successful foraging trip might be inclined to postpone departure after feeding the chicks.

Custer and Osborn (1978) found that herons from a North Carolina colony flew farther to feeding grounds during high tide. In this study, departure directions did not change with changing tides (Table 3). However, the data are limited, and since on tracking days the highest tides were at night, feeding areas were accessible in the lagoon at all observations. More observations, particularly at tidal extremes, might show that tides affected heron destinations in the lagoon and possibly departure directions. Further studies of heron foraging flights, especially under different ecological conditions, i.e., inland sites near lakes and rivers where water levels change relatively slowly, and at different times in the breeding cycle are needed to resolve the question of whether herons sometimes follow each other to feeding grounds.

Though these observations did not show that breeding adults followed others, a study of heron flights at other stages of the breeding cycle might produce different results. Perhaps during the pre-incubation period when nest attendance is less critical, herons find good feeding spots by following other birds. Or, if prey became unusually scarce or difficult to find, herons might resort to following neighbors on foraging flights. Late in the nesting

cycle flying young might tend to follow adults or each other. For a period varying from 1–3 weeks before reaching independence, young herons leave the nest for part of the day, but return to be fed by their parents (Pratt 1970). I have no data on the timing or directions of their flights but it seems possible that they might leave immediately after other herons and follow them from the colony.

Although the resources of the adjacent estuary were important to the colony, the feeding range of the herons at Audubon Canyon Ranch apparently encompassed a much wider area. None of the birds was marked and the destinations of those not landing in the lagoon is unknown, but the majority flew to other feeding grounds, perhaps at some distance. Some observers believe that Great Blue Herons may fly distances up to 80 km from nesting colonies to feeding grounds (Court 1908, Reinecke 1910, Miller 1943). Data on foraging flights at colonies with mixed species of herons and ibises suggest that long distance feeding flights are common in the Ciconiiformes (Dusi et al. 1971, Custer and Osborn 1978). Great Blue Herons fly about 40 km/h (Palmer 1962). Potential feeding grounds at the edges of Tomales Bay and San Francisco Bay, as well as in pastures and farm ponds, lie within 45 min flight of the colony in all directions taken by the herons (Fig. 1).

SUMMARY

Directions and timing of foraging flights of adult Great Blue Herons did not indicate that they followed each other from the colony to feeding grounds. Some herons apparently went directly to predetermined feeding areas, while others joined aggregations in the adjacent estuary. Herons on less than half of the departures went to the estuary. The majority appeared to be flying to other more distant feeding grounds. Herons incubating or attending small young left promptly, whereas herons at nests with older, unattended young tended to linger in the colony.

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